WOOD ANATOMY OF NOTEWORTHY SPECIES OF *LUDWIGIA* (ONAGRACEAE) WITH RELATION TO ECOLOGY AND SYSTEMATICS[1]

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ABSTRACT

Ludwigia anastomosans, a tree to 10 m, is studied because it is unusual in the genus in its arborescent habit. It proves to have unusually wide vessels; it also has interxylary phloem, hitherto reported for only one species of the genus. Wood anatomy of *Ludwigia peduncularis* and *L. torulosa* shows that they may be more closely related than so far indicated. Vestigial bars on perforation plates of *L. torulosa* are the first observed in Onagraceae and are believed to represent an instance of paedomorphosis, but also retention of a primitive feature. Other indicators of paedomorphosis in *Ludwigia* are abundance of erect ray cells and notably long vessel elements. The hypothesis that degree of vessel grouping is related to ecology in taxa having fiber-tracheids or libriform fibers is validated by *Ludwigia*, which has the lowest degree of vessel grouping for the family and is essentially aquatic. Other anatomical features reflective of ecology, combined in the Mesomorphy ratio, present a not dissimilar pattern that can be integrated with that given by vessel grouping if one takes into account probable transpiration rates and temperature regimes as well as water availability.

Data on wood anatomy of eight species of *Ludwigia* have been presented earlier (Carlquist, 1975, 1982a). That number seems small unless one takes into account the fact that *Ludwigia* is predominantly herbaceous; the most familiar species are nonwoody herbs of very wet habitats such as ponds, ditches, and streams. One of the species in the present study is a notable exception: *L. anastomosans* (DC.) Hara is a tree. The data on the collection studied here describe it as a tree 10 m tall with a trunk 15 cm dbh. Wood anatomy is of special interest because of this habit. In fact, the results obtained below demonstrate that the wood of *L. anastomosans* differs appreciably from that of other *Ludwigia* species.

Dr. Elsa Zardini, who collected the material of *L. anastomosans*, also kindly supplied material of two other species because she wished to see if wood anatomy demonstrated the degree of relationship between them. Dr. Zardini has contemplated the idea that *L. peduncularis* (Griseb.) Gómez may be closely related to *L. torulosa* (Arn.) Hara.

The wood anatomy of *Ludwigia* is of considerable interest with respect to ecology because *Ludwigia* characteristically grows in very wet places. *Ludwigia anastomosans* was collected in bamboo clumps by a blackwater stream in the Parque Natural de Caraca, Minas Geraes, Brazil. The material of *L. peduncularis* came from ditches near Havana, Cuba. The *L. torulosa* specimen was collected in a natural pond 17 km south of Tumeremo, Distrito Roscia, Estado Bolívar, Venezuela. In taxa with libriform fibers such as Onagraceae, Carlquist (1984a) hypothesized degree of vessel grouping to be in direct proportion to adaptation to dry conditions. In this case *Ludwigia* species ought to exhibit a low degree of vessel grouping. Although figures for vessels per group were developed in the earlier survey of woods of the family (Carlquist, 1975), no comparisons were made between those figures and ecological regimes occupied by the various species.

Ludwigia is a group of interest with relation to paedomorphosis in wood anatomy. This is, in turn, related to habit and ecology. The species in the present study were examined in this context to see if woodiness in *Ludwigia* is primary or secondary.

Although a study on wood anatomy can be expected to reveal new records for anatomical features, two in the present study proved of especial interest and worthy of discussion: occurrence of interxylary phloem and presence of vestigial bars on some perforation plates.

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MATERIALS AND METHODS

Voucher specimens are located at the Missouri Botanical Garden. Appreciation is expressed to Dr. Elsa Zardini for providing dried wood samples suitable for study. For *L. peduncularis* and *L. torulosa,* samples represented basal portions, but diameter was small (2 and 4 mm, respectively). The material of *L. anastomosans* was from a branch about 1.5 cm in diameter. Although this is much less than the 15 cm diameter reported for trunks of this species, the branch material is considered here to represent an essentially mature pattern.

Woods were boiled in water, stored in 50% ethyl alcohol, and sectioned on a sliding microtome. Sections prepared in this way were, in part, satisfactory, but cell collapse on account of thinness of wood cells was excessive in some instances. Therefore an alternative method involving further softening, embedding in paraffin, and sectioning on a rotary microtome (Carlquist, 1982b) was employed. Sections prepared by both techniques were stained in a safranin–fast green combination. Macerations were prepared with Jeffrey's Fluid and stained with safranin.

Means are based upon 25 measurements (fewer if feature is scarce) except for vessel wall thickness, libriform fiber diameter, and libriform fiber wall thickness, in which a few typical cells were measured. Vessel diameter includes the wall, although lumen diameter may be preferable for some purposes and may be calculated by subtracting wall thickness from the data presented here. Mean values for vessel grouping are obtained on the following basis: a solitary vessel = 1.0, a pair of vessels in contact = 2.0, etc. Bark was not observed specifically in the present study, although sections of the stem of *L. torulosa* included portions of the spongy stem covering that proves to be aerenchyma like that figured for "*Jussiaea repens*" L. (now a *Ludwigia*) by Metcalfe & Chalk (1950), and studied in detail by Ellmore (1981) for *L. peploides* (HBK) Raven.

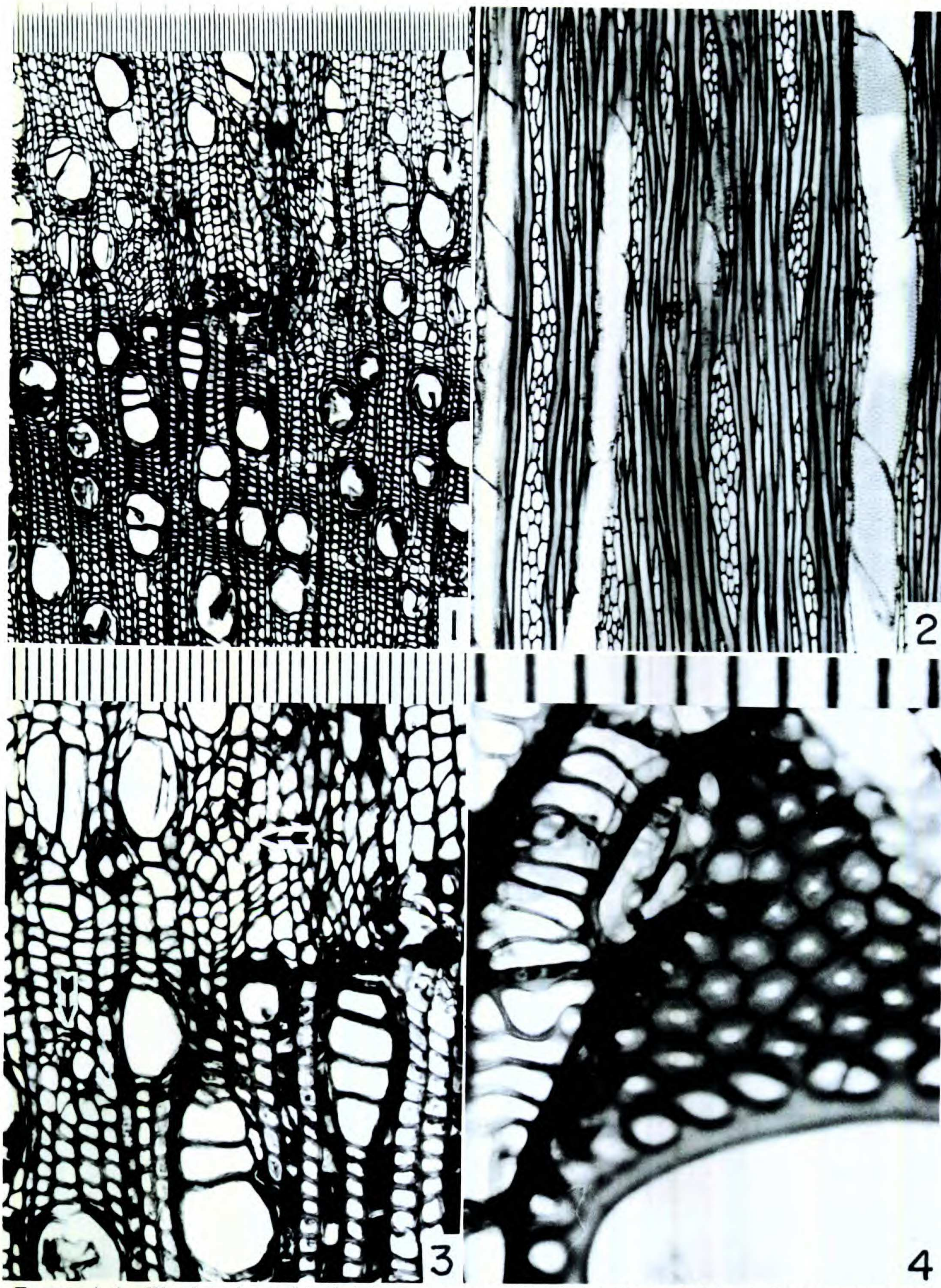
ANATOMICAL DESCRIPTIONS

Ludwigia anastomosans (DC.) Hara, *Zardini & Gentry 2175* (Figs. 1–6).

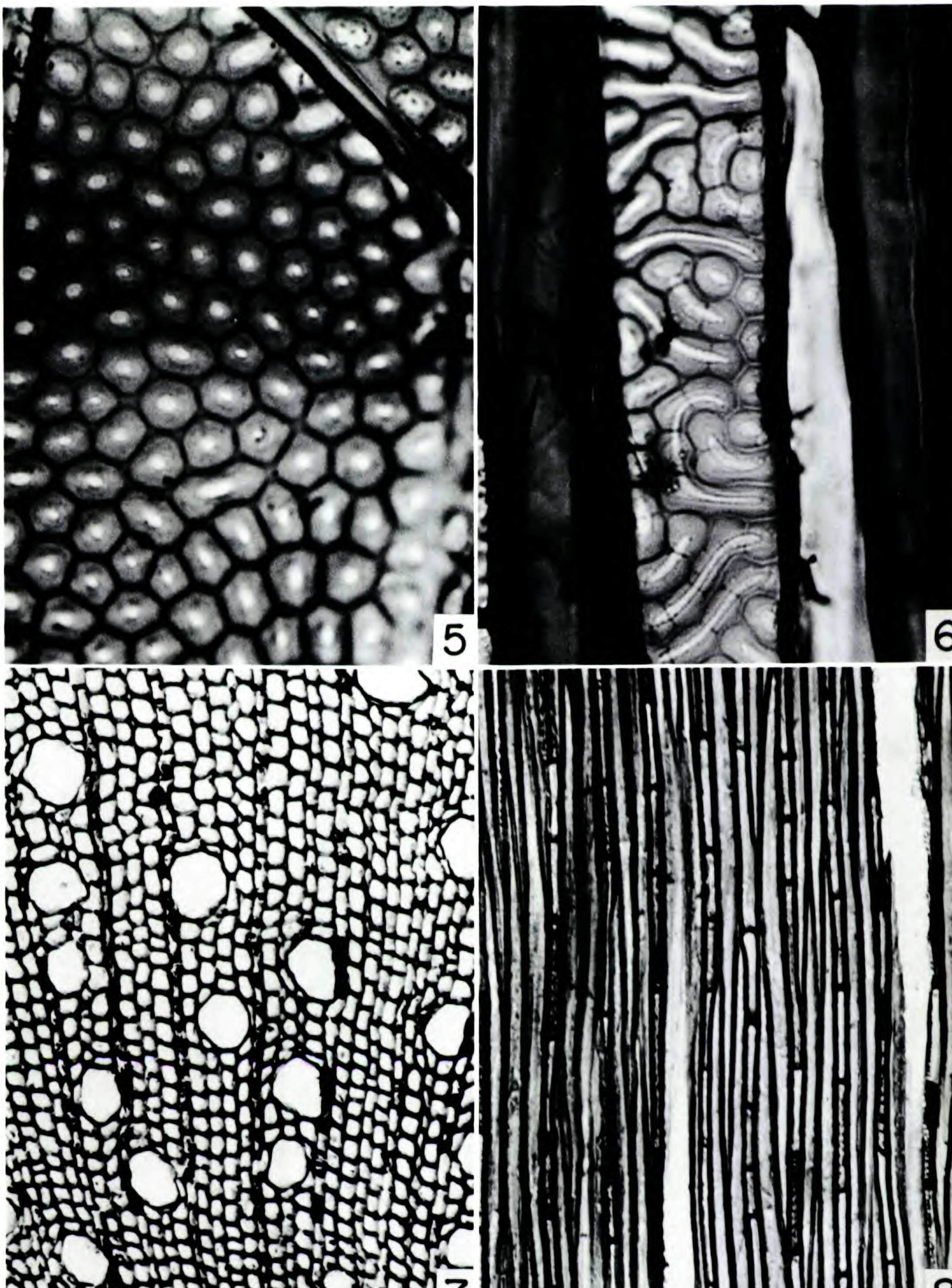
Growth rings inconspicuous, and probably related to water level of the riparian habitat (Fig. 1). Mean number of vessels per mm^2, 51. Mean number of vessels per group, 1.24; vessels tending to be grouped into radial multiples (Figs. 1, 3). Mean vessel diam., 109 μm. Mean vessel wall thickness, 2.5 μm. Mean vessel element length, 458 μm. Perforation plates simple (Figs. 2, 4). Lateral wall pitting of vessels alternate, pits crowded and circular to polygonal in outline, about 12 μm diam. on vessel–vessel interfaces (Figs. 4, 5). Vessel–axial parenchyma and vessel–ray pitting alternate to scalariform, pit apertures long (sometimes scalariform), pit apertures wide ("gaping"). Pitting with relatively conspicuous vesturing on vessel–vessel pits (Fig. 5, upper right), vesturing less pronounced on vessel–axial parenchyma and vessel–ray pits. Occasional vessel–vessel pits in aberrant patterns (Fig. 6). Tyloses abundant (Figs. 1, 3). Imperforate tracheary elements all libriform fibers because pits apparently simple, although a few exceptional pits with small borders also observed. Many libriform fibers septate. Mean libriform fiber diam., 28 μm. Mean libriform fiber wall thickness, 2.3 μm. Mean libriform fiber length, 588 μm. Numerous libriform fibers with gelatinous walls (Fig. 6) and therefore probably reaction wood. Axial parenchyma vasicentric scanty. Bands of phloem-containing axial parenchyma present in marginal positions (end of growth rings) or scattered without any relation to growth rings (Figs. 1, 3). Rays multiseriate and uniseriate, the former slightly more frequent (indicated by relative heights in Fig. 2). Ray cells predominantly erect and square (Fig. 2), a few procumbent cells present in multiseriate portions of multiseriate rays. Mean multiseriate ray height, 2,707 μm. Mean uniseriate ray height, 349 μm. Mean width multiseriate rays at widest point, 3.95 cells. Ray cell walls moderately thin, lignified. Wood nonstoried. Raphides present in phloem-containing axial parenchyma strands.

Ludwigia peduncularis (Griseb.) Gomez, *Ekman 13416* (Figs. 7, 8).

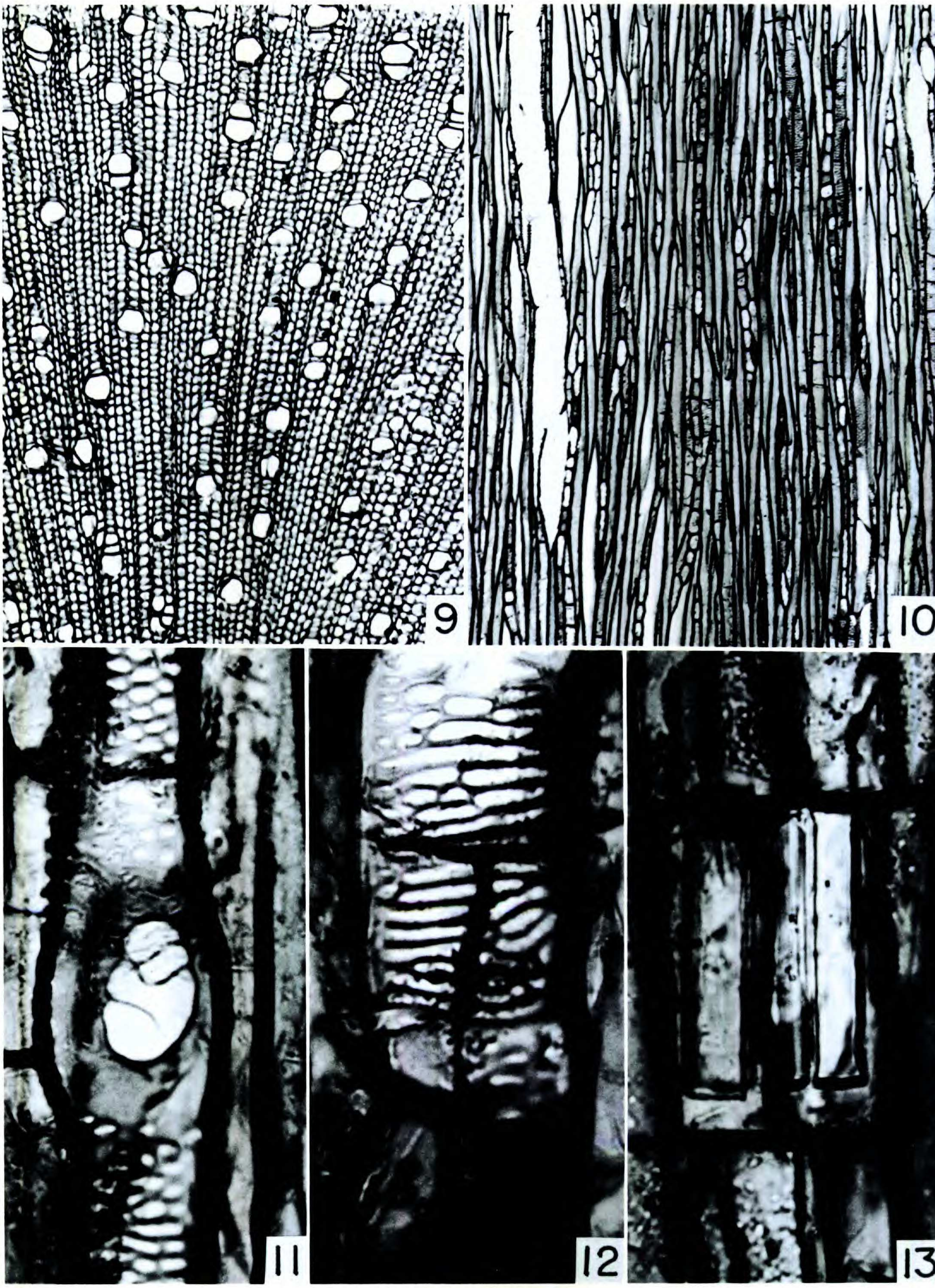
Growth rings absent (portion studied probably less than one year's accumulation). Mean number of vessels per mm^2, 62. Mean number of vessels per group, 1.30. Mean vessel diam., 50 μm. Mean vessel wall thickness, 1.8 μm. Mean vessel element length, 484 μm. Perforation plates simple. Lateral walls of vessels with crowded alternate elliptical pits (about 4 × 8 μm) with pointed ends and narrow apertures (vessel–vessel contacts). Vessel–axial parenchyma and vessel–ray pitting similar but with pits longer (appearing pseudoscalariform) and wider, and with wider



FIGURES 1–4. Wood sections of *Ludwigia anastomosans, Zardini & Gentry 2175.*—1. Transection; termination of growth ring occurs in the middle of the photograph.—2. Tangential section; multiseriate rays are wide, more numerous than uniseriate rays.—3. Portion of transection, showing strands of interxylary phloem (arrows) and vessels in radial multiples.—4. Portion of vessel wall from tangential section; intervascular pitting and perforation plate rim, below; axial parenchyma cells, upper left. Figures 1, 2, magnification scale above Figure 1 (finest divisions = 10 μm); Figure 3, divisions = 10 μm; Figure 4, divisions = 10 μm.



FIGURES 5–8. Wood sections of *Ludwigia*. 5, 6. *L. anastomosans, Zardini & Gentry 2175*. —5. Intervascular pitting from tangential section, showing transition between circular and polygonal pit shapes; vesturing evident in pits at upper right. —6. Portion of vessel and associated cells from tangential section; note aberrant pit and pit aperture configurations and splits in gelatinous fiber walls (right). 7, 8. *L. peduncularis, Ekman 13416*. —7. Transection; vessels solitary; dark-colored deposits in ray cells. —8. Tangential section; all rays are uniseriate. Figures 5, 6, magnification scale above Figure 4; Figures 7, 8, magnification scale above Figure 3.



FIGURES 9–13. Wood sections of *Ludwigia torulosa, Holst, Steyermark & Manara 2257.*—9. Transection; libriform fibers are thin-walled.—10. Tangential section; multiseriate rays are narrow, less frequent than uniseriate rays.—11. Portion of radial section showing vestigial bars on a perforation plate.—12. Portion of a radial section showing vessel–ray pitting.—13. Portion of a radial section showing rodlike crystals in two ray cells. Figures 9, 10, magnification scale above Figure 1; Figures 11–13, scale above Figure 4.

apertures. Pits of vessels vestured, less so in vessel–axial parenchyma and vessel–ray contacts than on vessel–vessel pitting. Imperforate tracheary elements all libriform fibers, the pits minute, apparently simple. Libriform fibers mostly septate. Mean libriform fiber diam., 18 μm. Mean libriform fiber wall thickness, 1.2 μm. Mean libriform fiber length, 778 μm. About half of the wood consisting of gelatinous fibers (Fig. 7), therefore apparently reaction wood. Axial parenchyma vasicentric scanty, very few strands adjacent to each vessel (or some vessels with no adjacent axial parenchyma). Interxylary phloem absent. Rays almost all uniseriate (Fig. 8). Ray cells all erect. Mean uniseriate ray height, 1,566 μm. Ray cells moderately thin-walled but lignified (Fig. 8). Wood nonstoried. No crystals observed. Axial parenchyma and ray cells containing droplets or massive accumulations of a brownish substance (Figs. 7, 8).

Ludwigia torulosa (Arn.) Hara, *Holst, Steyermark & Manara 2257* (Figs. 9–13).

Growth rings absent (portion studied probably less than a year's accumulation). Mean number of vessels per mm^2, 62. Mean number of vessels per group, 1.55. Mean vessel diam., 55 μm. Mean vessel wall thickness, 1.6 μm. Mean vessel element length, 374 μm. Perforation plates mostly simple, but some with modified or vestigial bars (Fig. 11). Lateral walls of vessels with alternate polygonal pits about 5 μm diam. on vessel–vessel contacts. Vessel–axial parenchyma and vessel–ray pits alternate, opposite, or scalariform, larger and with wider apertures than the vessel–vessel pits (Fig. 12). Vestures dense within cavities of vessel–vessel pits, somewhat less abundant on vessel–axial parenchyma and vessel–ray pits. Imperforate tracheary elements all libriform fibers, because the pits apparently simple. Libriform fibers nonseptate, but starch present in them. Mean libriform fiber diam., 25 μm. Mean libriform fiber wall thickness, 1.5 μm. Mean libriform fiber length, 538 μm. Libriform fiber walls somewhat gelatinous. Axial parenchyma vasicentric scanty, often only one strand adjacent to a vessel. Rays multiseriate and uniseriate, uniseriates more abundant (Fig. 10). Ray cells mostly erect, a few square cells present. Mean multiseriate ray height, 1,188 μm. Mean uniseriate ray height, 270 μm. Mean multiseriate ray width at widest point, 2.2 cells. Cell walls moderately thin but lignified. Wood nonstoried. Large rodlike crystals (one tip concave, the other convex, suggesting paired crystals) present in a few ray cells (Fig. 13).

CONCLUSIONS

HABIT AND ECOLOGY

In a given floristic area, wider vessels characterize trees as compared with shrubs and subshrubs (Carlquist & Hoekman, 1985). In a genus or family that ranges into diverse habitats, tropical tree species tend to have the widest vessels (e.g., Vliet, 1979). *Ludwigia anastomosans* has notably wide vessels for the family Onagraceae. Mean vessel diameter in this species equals the widest mean diameter reported in the earlier survey (Carlquist, 1975), a fact very likely related both to its arboreal nature and tropical habitat. The figure recorded for vessel diameter in *L. anastomosans* may be conservative, because the stem studied is relatively small compared with the large diameter of trunks of these trees. In trees, vessel diameter is greater at the periphery of older stems (e.g., Carlquist, 1984b).

The abundance of erect ray cells in comparison with procumbent ray cells in *Ludwigia*, even in *L. anastomosans*, suggests that *Ludwigia* may represent some degree of secondary woodiness. This idea was entertained for *Ludwigia* earlier (Carlquist, 1975). The presence of a few vestigial bars on perforation plates in *L. torulosa* (Fig. 11) is pertinent in this regard. Presence of a few such plates does suggest retention of primitive features in the primary xylem (the "refugium" theory of Bailey, 1944), but it also suggests that this feature is carried forward into the secondary xylem by virtue of paedomorphosis. Paedomorphosis is indicated by erect ray cells and the relatively long vessel elements (Carlquist, 1962), two features well displayed in *Ludwigia*. Presence of occasional scalariform perforation plates in otherwise specialized wood by virtue of paedomorphosis is illustrated in a few other predominantly herbaceous groups such as Campanulaceae (Shulkina & Zikov, 1980), *Crepidiastrum* of the Asteraceae (Carlquist, 1983a), or *Patrinia* of the Valerianaceae (Carlquist, 1983b). The presence of scalariform perforation plates is, however, more primitive than presence of simple plates exclusively.

In an earlier paper (Carlquist, 1984a), vessel grouping in taxa with libriform fibers (as in Onagraceae) or fiber-tracheids was held to be proportional to adaptation to dry conditions. This hypothesis is worth testing in Onagraceae, because of the wide range of ecological circumstances occupied by its members. Data on vessel grouping were prepared earlier for the family (Carlquist, 1975), and indices designed to enable comparison with ecological conditions were devised (Carlquist, 1977). These data can now be analyzed in the light of the vessel grouping hypothesis. Vessel grouping figures were not offered for six *Ludwigia* species studied earlier (Carlquist, 1982a), and so are presented here: *L. bullata* (Hassler) Hara, 1.08; *L. elegans* (Cambess.) Hara, 1.36; *L. peruviana* (L.) Hara, 1.10; *L. sericea* (Cambess.) Hara, 1.12; *L. tomentosa* (Cambess.) Hara, 1.04; *L.* sp. (aff. *L. longifolia*), 1.23.

The mean value for vessel grouping in the 12 collections of *Ludwigia,* sole genus of tribe Jussieeae, is 1.23. The next lowest value, by tribe, occurs in Hauyeae (1.67), followed by Fuchsieae (1.80) and Epilobieae (1.85); data for Lopezieae and Onagreae were subdivided into habit categories. If one considers that the aquatic habitats characteristic of *Ludwigia* species represent the most mesic ecological situations of the family, vessel grouping is a more accurate indicator of ecology within Onagraceae than the indices "Vulnerability" or "Mesomorphy." However, one should take into account that the Mesomorphy figure for Hauyeae (1,242), which seems high compared with that for 12 collections of *Ludwigia* (415), is related to the wide vessels in that tribe, which in turn is doubtless characteristic for a species transpiring large volumes of water in a warm, moist tropical forest. Both of these figures are much higher than for groups in the family occupying drier habitats, such as annuals of tribe Onagreae (161) or caudex perennials of Onagreae (48).

SYSTEMATICS

The data provided are consonant with the idea that *L. peduncularis* and *L. torulosa* may be closely related. These species have an unusual feature in common, the presence of rays exclusively or nearly uniseriate at the outset of secondary growth. The absence in *L. peduncularis* of the curious mirror-image crystals observed in *L. torulosa* is not considered decisive. Such crystals have been reported in *L. bullata, L. octovalvis,* and *L. peruviana* (Carlquist, 1975, 1982a). In turn, these crystals resemble the large, styloidlike crystals of *Hauya*; these latter crystals occur in axial parenchyma rather than in rays, as in *Ludwigia.* Data from wood anatomy should not be interpreted in too detailed a way here: variability within species is not known and not all species of all sections of *Ludwigia* have been studied. Wood anatomy is not often a decisive indicator of relationships at species and section (subgenus) levels.

The occurrence of interxylary phloem in *L. anastomosans* is noteworthy. Interxylary phloem has been reported previously for the genus only in *L. sericea* (Carlquist, 1982a), although it occurs elsewhere in the family (Carlquist, 1975). The significance of interxylary phloem seems to lie with seasonality in translocation of photosynthates, as noted earlier (Carlquist, 1975). Because *L. anastomosans* is a tree, presumably with an annual flowering season, production of interxylary phloem would be adaptive, whereas in an annual or short-lived perennial *Ludwigia* plant, the phloem from a single year, undiminished by crushing at the end of a season as in longer-lived plants, would probably suffice to channel photosynthates into flowers and developing fruits.

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